The distribution and abundance of Delphacidae (Homoptera) in central Argentina

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Abstract: A 3-year field study has been carried out on the distribution and abundance of Delphacidae in central Argentina. Insects were collected along a 300 km transect of seven equally spaced sampling sites. At each sampling station there was one sticky trap 6 m above the ground and five sticky traps 1.5 m above the ground. The sampling frequency was every 6 to 15 days during the spring and summer months and monthly during the rest of the year. *Delphacodes kuscheli* (vector of a local strain of the maize rough dwarf virus, MRDV-RC), *Delphacodes haywardi, Delphacodes balboae, Toya* spp., *Dicranotropis nigricula* and *Sogatella kolophon meridiana* were collected. Among them, *D. kuscheli* and *Toya* spp. comprised 67 and 26% of all the delphacid captured. *Delphacodes kuscheli* showed a geographical gradient in abundance, coincident with the land management gradient which showed a very heterogeneous landscape (in terms of crop species and land management) dedicated to grain production in the north-eastern part of the study area and a less heterogeneous landscape dedicated to cattle breeding (with large extensions covered with pastures where *D. kuscheli* reproduces and overwinters) in the south-west. *Delphacodes kuscheli* showed a high dispersal ability and synchronic dynamics, whereas *Toya* spp. showed a lower dispersal ability with less synchronic dynamics. The implications for the MRDV-RC transmission is discussed.

1 Introduction

The list of species of Delphacidae present in central Argentina includes *Delphacodes balboae, Delphacodes haywardi, Delphacodes kuscheli, Delphacodes lata, Toya argentinensis, Toya propinqua, Dicranotropis nigricula* and *Sogatella kolophon meridiana* (REMES LENICOV and VIRLA, 1993). Among them, the most important is *D. kuscheli*, as it is a proven vector of a local strain of the maize rough dwarf virus (MRDV-RC), an endemic disease of maize crop causing important losses in central Argentina (MARCH et al., 1995). Although *D. kuscheli* is the only species with an experimentally demonstrated capacity for virus transmission, doubts about the potential of other species that have the same capacity (more precisely *T. propinqua*), exist.

A number of field studies have shown a relatively wide range of different crops (maize, wheat and sorghum) and/or weed species infected with the MRDV (*Digitaria sanguinalis, Sorghum halepense, Cynodon dactylon, Echinocloa colonum* and *Cyperus* sp.; LAGUNA et al., 1991), that are included in the host plant range of Delphacidae in the same study area (PELUC et al., unpublished data). Previous reports pinpointed the importance of weeds surrounding the maize plots as a source of insects, to colonize the crop at an early stage, when the seedlings are most susceptible to the virus infection. However, studies on the spatial arrangement of infected plants (TRUMPER et al., 1991, 1996) showed that there is no evidence to support that view. Recently GRILLI and GORLA (1997) have shown that there is a temporal and spatial covariation between the nor-

malized difference vegetation index (NDVI, measured from the NOAA-AVHRR meteorological satellite sensor) and *D. kuscheli* abundance. As the NDVI is related with the amount of land occupied by oat crops (the main overwintering host of the vector) and other natural pastures, they suggested that maize plot colonization is a regional process, probably more affected by the spatial interspersion of maize and natural and cultivated pastures than the proximity of weeds surrounding the maize plots.

In general, the abundance of the delphacid species occurring in central Argentina has been studied on a local scale, and only in economically important species such as *D. kuscheli* (TESON and REMES LENICOV, 1989; REMES LENICOV and VIRLA, 1993).

During the last 50 years the only studies made on Delphacidae as a whole group in Argentina, were descriptive and taxonomic (REMES LENICOV and VIRLA, 1993).

However, understanding distributional and abundance patterns may require work on a wider geographic scale to uncover population properties that could not be perceived on a smaller scale. This is why for the first time the distribution and abundance of the whole Delphacidae group is analysed for a wide region of Argentina.

The average host plant range of leafhoppers is wider in ephemeral rather than in permanent habitats. The majority of trophic interactions between leafhoppers and host plants found in ephemeral habitats involve polyphagous leafhoppers, whereas the opposite pattern prevails in permanent habitats. The difference between

the average host plant range width of leafhoppers in permanent and ephemeral habitats results from a larger number of polyphagous leafhoppers per plant in the ephemeral habitats (NOVOTNÝ, 1994a). Leafhoppers on ruderal plants have a higher dispersal ability, a wider range of host plants, a larger geographical distribution and more generations per year than species on competitive and stress-tolerant plants. These features evolved independently at least within Delphacidae and Cicadelidae (NOVOTNÝ, 1995). Novotný's hypothesis proposes that in temporal habitats, density-dependent production of macropters in wing dimorphic species is an adaptation to frequent deterioration of habitat caused by factors independent of the density of species. The predominance of brachypters in permanent habitats indicates that a density-dependent decrease in fitness usually does not offset the potential decrease in fitness connected with macroptery and dispersal (NOVOTNÝ, 1994b).

In this study, the spatial and temporal distribution and abundance patterns of the species of Delphacidae at a subregional geographical scale, along a transect within central Argentina (including endemic and non-endemic areas of MRDV-RC transmission), was analysed to verify the delphacid assemblage along an agricultural gradient of the study region.

2 Methods

Insect sampling was carried out according to the description of GRILLI and GORLA (1997). Briefly, insects were sampled using sticky traps, at a frequency of 6–15 days during the spring and summer seasons and monthly during the cold seasons. Trapping was carried out along a transect of approximately 300 km, at seven roughly equally spaced sampling sites. Sampling started on October 1992 and finished on April 1995. Insect trapping was made at two levels above the ground, 1.5 and 6 m. The working hypothesis was that the insects collected by traps nearer the ground would have a stronger dependence on the insect fauna associated with the particular vegetation patch over which the trap was installed, whereas the insects collected by the high traps would have a weaker dependence on the local vegetation, but would show patterns of the long-distance dispersal of the insects. The sticky traps consisted of metal cylinders supporting a plastic film painted with an adhesive. The plastic film was replaced by a clean one on each sample date. The films were transported to the laboratory, where the insects were identified to species according to REMES LENICOV and VIRLA (1993). On each sampling site, a set of one high trap and five low traps were installed close to each other (maximum of 100 m separation between the most distant traps of the set), with no special relation to the surrounding vegetation.

The sampling sites were located along a transect with a north-eastern extreme at 31 51.947'S 63 44.711'W, and a south-western extreme at 33 35'S 65 25'W (latitude and longitude, respectively) (fig. 1). The region crossed by the transect shows two different land management areas associated with different soil types. The northern part is mainly used for grain production, whereas the southern part is mainly used as a cattle breeding area, interspersed with patches of crop production.

Because of the insect capture technique, abundance estimates refer to the dispersal of individuals at 1.5 and 6 m above the ground level. Species density was estimated as the number

of insects per unit trap surface per day of trap exposure. All the analysis were based on log (x + 1) transformed data.

The proportion of D. kuscheli, in each sampling station for the whole sampling period, was studied in relation to the surface (in hectares) planted with grain crops and natural and cultivated grasses, taken from the last National Agronomic Census (INDEC, 1988), to investigate the association between land use management and the proportion of D. kuscheli in that place.

The mean and the variance of the abundance per year was estimated for each species in each sampling site. Then the mean abundance per year was compared with the variance observed during that year.

3 Results

The individuals collected belonged to the following delphacid species: D. kuscheli, D. balboae, D. haywardi, Di. nigricula, T. propinqua, T. argentinensis, and Sogatella kolophon meridiana. Toya propinqua and T. argentinensis could not be separated for all the samples, and are considered together in the rest of this paper. All species showed marked seasonal variations, increasing in abundance from spring (October), to decrease in autumn (March).

In general, the species abundance decreased during the study period. It was more marked in Di. nigricula, D. haywardi and Sogatella k.m., which practically disappeared in the third year. It was less marked in D. kuscheli, D. balboae and Toya spp., that showed a similar abundance during the first 2 years, but a drop during the third. The same pattern was observed in high (fig. 2) and low (fig. 3) traps, with minor variations. The number of species decreased from the north.

Delphacodes kuscheli was by far the most abundant species, representing 67% of the total captures during the study period. The density of this species increased in relative (out of all delphacids) and absolute terms from north to south (nonendemic to endemic areas of MRDV-RC transmission). In relative terms, it represented 27% of the insects in the north, increasing towards the south to reach 77%. In absolute terms, the average density (over trap types and years) in the northernmost station was 0.035, increasing to more than 0.2 in the southern stations (fig. 4). Delphacodes kuscheli showed only one abundance peak per season, that occurred around the same dates on different years (first 2 weeks of December during the first studied season and first week of January during the subsequent 2 years). This abundance peak occurred simultaneously on all sampling sites, always before the abundance peak of Toya spp.

The Toya spp. group was the second most important, representing 26% of the total. Along the transect, the density of Toya spp. was maintained in relation to the total delphacids, around 30–40% in all stations except in the southernmost one (Mercedes), where it dropped to 14% of the total. In absolute terms, the average density (over trap types and years) was similar for all the stations (around 0.05), except in Travaglia station where it reached 0.14 (fig. 4). The abundance peak of Toya spp. occurred in January each year, with higher variability in peaking dates, compared with D. kuscheli,
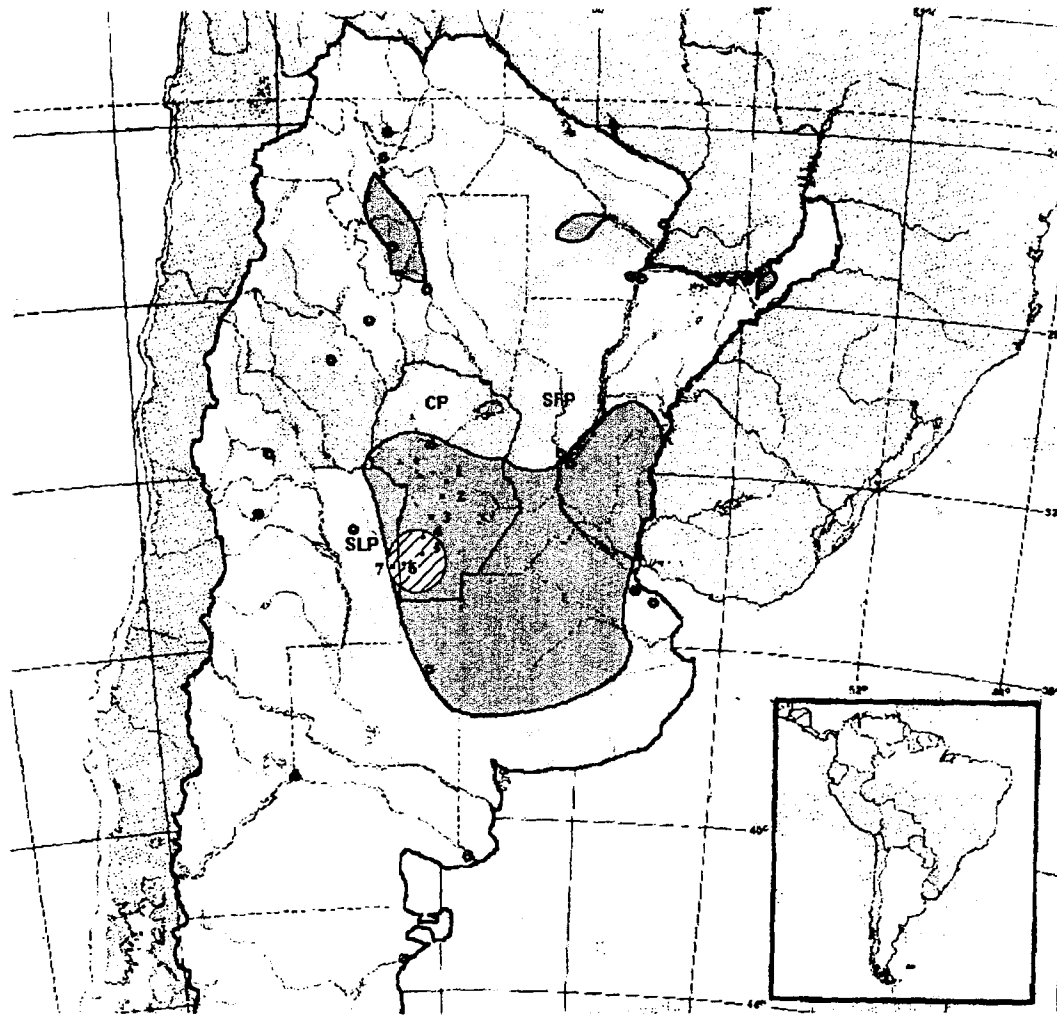
Fig. 1. Geographic location of the study area and sampling sites. 1: Manfredi sampling station; 2: Tancacha sampling station; 3: Cabrera sampling station; 4: Espinillo sampling station; 5: Holmberg sampling station; 6: Travaglia sampling station; 7: Mercedes sampling station. Hatched area: Rio Cuarto Disease endemic area; Grey area: Maize productive area of Argentina. CP: Córdoba Province; SLP: San Luis Province; SFP: Santa Fé Province

and without the synchronicity among sampling sites shown by *D. kuscheli*.

Delphacodes balboae represented 5% of the insects captured during the whole study period. The species decreased in relative abundance, from 19% in the north to 4% in the south. The average absolute density also showed a decrease from north to south (0.025 to 0.011) (fig. 4).

Sogatella kolophon meridiana was the rarest species, representing 0.1% of the total capture, and because of the low number, it was difficult to discern any pattern. *Di. nigricula* and *D. haywardi* represented 1.4 and 0.7% of the total capture, respectively. They both showed a decreasing tendency from north to south of the study transect. These three species appeared mostly (71% of the total individuals) during the first study period (October 1992–March 1993), coinciding with an unusual occurrence of delphacid nymphs in the high traps at the beginning of December 1992, and they did not occur at all during the third study period (fig. 4).

When considering the relationship between the average abundance in each sampling site for a particular species within an individual growing season (October to March) and its temporal variance, all species showed the same significant linear relationships for the 3 years studied (i.e. the relation between density variation over space with temporal variation appeared constant over the study period, fig. 5). Additionally, the slope of this relation between average density and its temporal variation was positively related with the overall abundance of each species density, showing that the higher the species density, the higher its temporal variation. In all cases, the slope of the relationship between variance and average always had values lower than two.

Aggregating data over all sampling stations, high and low traps captures of *D. kuscheli* showed a significant linear relation, with the high traps capturing 1.23 times more insects per surface and time unit than low traps (fig. 6). This relationship (measured by R^2) was significant (except for Manfredi sampling site), and showed
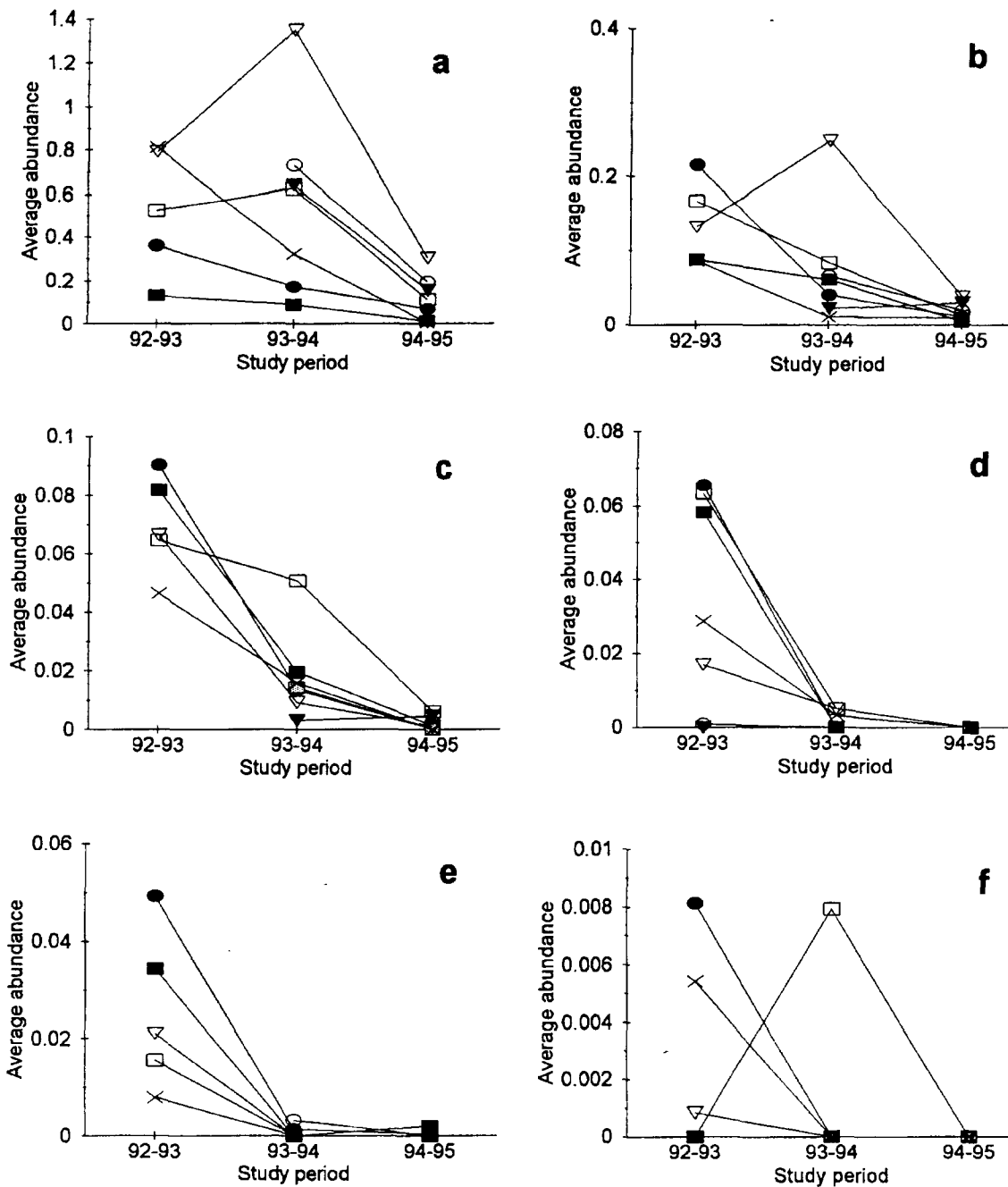
Fig. 2. Seasonal average abundance for the species captured by the 6 m sticky traps during the 3-year study. a: D. kuscheli, *b:* Toya spp., *c:* D. balboae, *d:* Dicranotropis nigricula, *e:* D. haywardi, *f:* Sogatella k.m. *Symbol references:* ■, *Manfredi;* ●, *Tancacha;* □, *Cabrera;* ○, *Espinillo;* ▼, *Holmberg;* ∇, *Travaglia;* ×, *Mercedes*

an almost constant slope of 0.64 (high traps as the 'independent' variable) on each sampling station, showing that sampling sites did not interact with trap types (ANOVA, P > 0.05) (table 1).

In *Toya* spp., the relationship between high and low trap captures was lower than the relation observed in *D. kuscheli* (R² = 0.43), although with a significant slope showing that low traps captured 1.7 times more insects than the high ones (fig. 6). Analysing the relation by sampling site, Manfredi and Cabrera (northern area)

showed no significant relation, whereas Espinillo, Travaglia and Mercedes showed a highly significant linear relation (R² ranging from 0.63 to 0.83) and slopes from 1.9 to 3.2, increasing to the south (table 2). On each sampling site, high and low traps captured approximately the same number of insects (all species) (ANOVA, P > 0.05).

The correlation between the proportion of *D. kuscheli* and the hectares of annual crops for each sampling site was significative and showed a negative slope
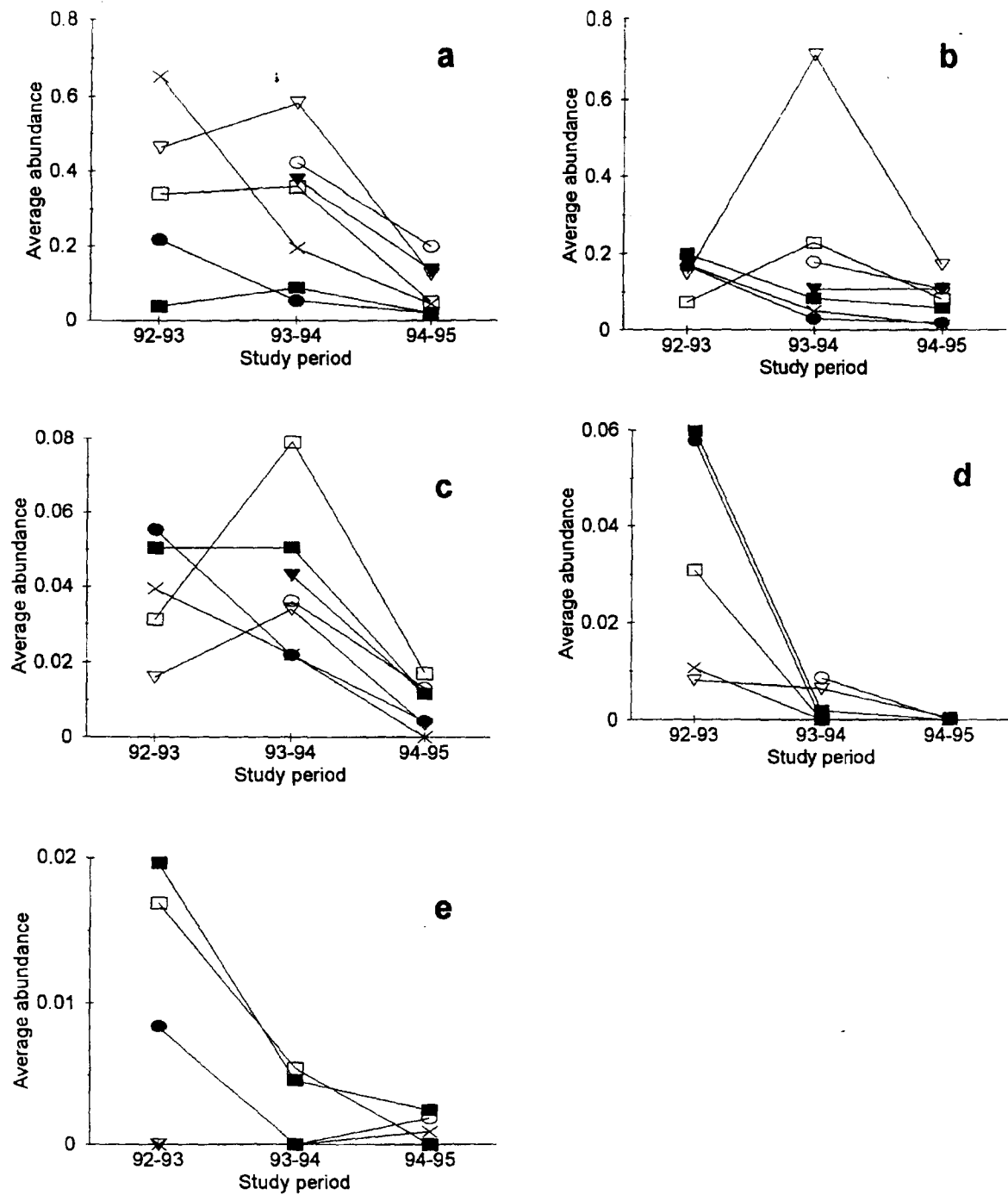
Fig. 3. Seasonal average abundance for the species captured by the 1.5 m sticky traps during the 3-year study. a: D. Kuscheli, b: Toya spp., c: D. balboae, d: Dicranotropis nigricula, e: D. haywardi, f: Sogatella k.m Symbol references: ■, Manfredi; ●, Tancacha; □, Cabrera; ○, Espinillo; ▼, Holmberg; ▽, Travaglia; ×, Mercedes

(Y = 0.84096 − 0.00639 × x; r = 0.88;, P < 0.05). The correlation between the proportion of *D. kuscheli* and the hectares of natural and cultivated grasses for each sampling site was significant and showed a positive slope (Y = 0.195786 + 0.0126 × x; r = 0.90; P < 0.05). These correlations also showed that the abundance of annual crops (measured as hectares planted) decreases to the south of the region studied and the abundance of

natural and cultivated grasses increases to the south of the transect (fig. 7).

4 Discussion

Among the species of Delphacidae in the studied area, *D. kuscheli* was by far the most abundant with the
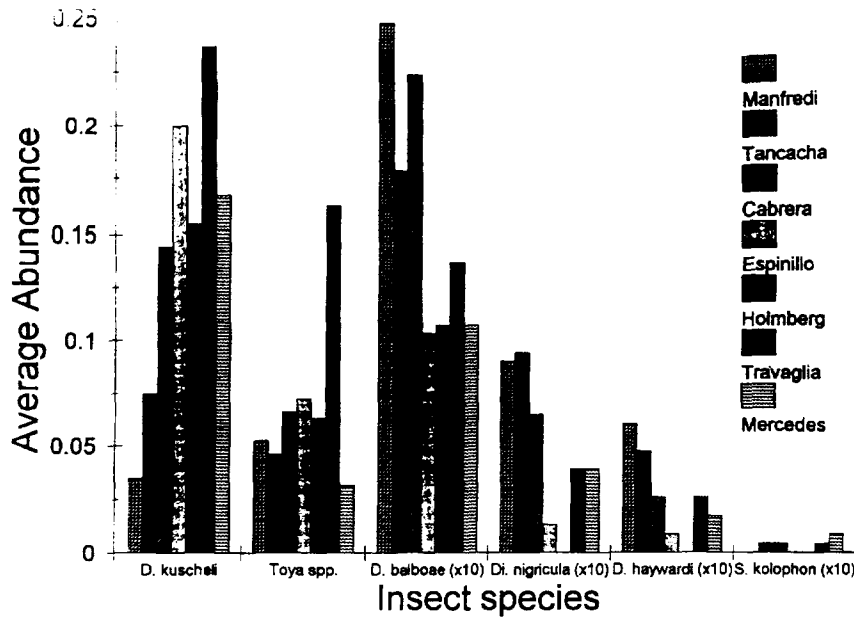
Fig. 4. Average density (over the study period and trap types) by species and sampling sites; D. kuscheli, Toya spp., D. balboae, Dicranotropis nigricula, D. haywardi, Sogatella kolophon meridiana
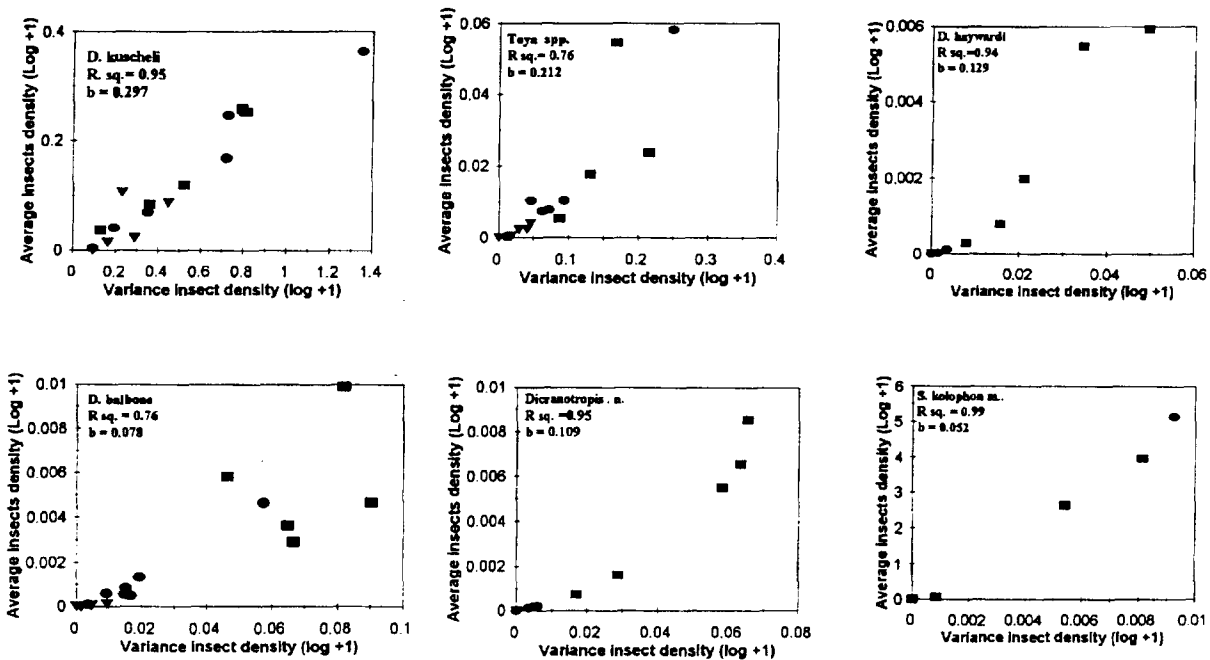

Fig. 5. Relationship between average and variance density by season for each species. D. kuscheli, Toya spp., D. balboae, Dicranotropis nigricula, D. haywardi, Sogatella k.m. R sq.: correlation coefficient; b: slope

second most abundant group being *Toya* spp. *Di. nigricula*, *D. haywardi* and *Sogatella k.m.* were the least abundant species appearing mostly in 1992, coinciding with an unusual occurrence of delphacid nymphs in the high traps, and thus suggesting that they could passively disperse long distances only under special weather conditions.

All the species occurred with marked seasonality, increasing from October, peaking between December–January to decline afterwards and disappear from the strip 1.5–6 m above the ground during the winter. All

species showed a constant linear relation between the mean density and the temporal variance of each season, throughout the 3 years of the study, so conforming with Taylor's Power Law (Taylor, 1961). The temporal variability increased at a higher rate, according to the average abundance of each species. The constancy of this relationship, in spite of the general decrease in abundance of Delphacidae, is remarkably and indicates the existence of a process, external to the species population that repeats regularly over time.

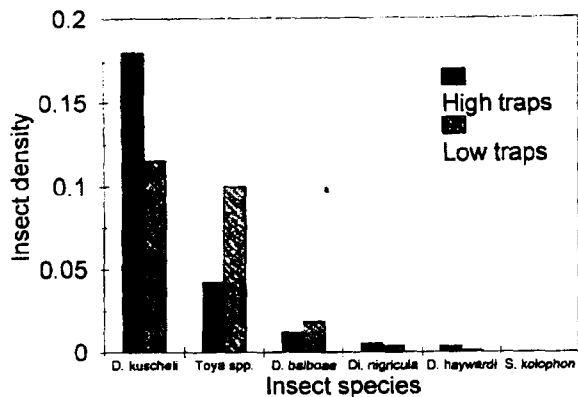Coincident with the findings of Power (1990), the

Fig. 6. Average density (over all sampling sites and study period) by species and trap type

environmental diversity (in term of crop species per unit area) showed a positive relation with the delphacid species diversity and a negative relation with the abundance of individual species (i.e. higher environmental and delphacid species diversity coupled with low density populations in the north-east and lower environmental and delphacid species diversity coupled with high density populations in the south-west).

Delphacodes kuscheli showed a remarkably abundance gradient from the north-east to the south-west of the study area. This gradient coincides with the gradient of MRDV-RC incidence and the agricultural land management. Within the southern area, the land is mainly used for cattle breeding, in which large, long-lasting plots with cattle pasture cover the areas, interspersed
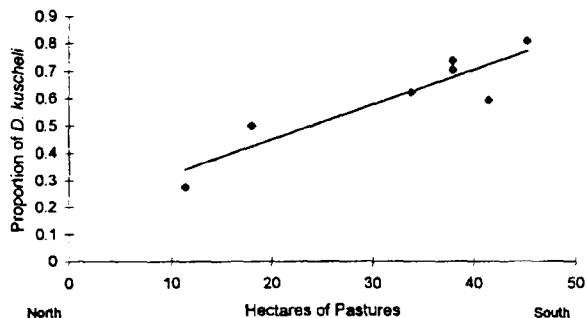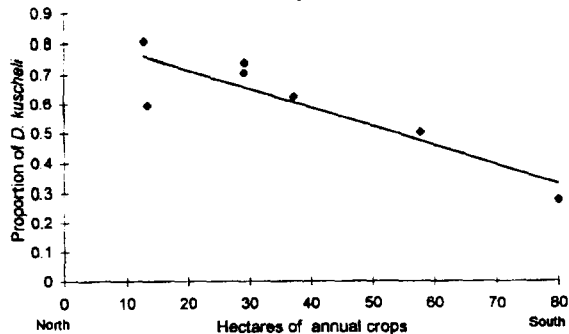
Fig. 7. Relationship between the proportion of D. kuscheli *captured in each sampling station and the hectares of annual crops (for grain) and pasture (for cattle) in each place according to the National Agronomic Census* (INDEC, 1988)

Table 1. Adjusted linear fits of the relation between high and low sticky traps, for D. kuscheli *captures*

				Sampling stations			
	Manfredi	Tancacha	Cabrera	Espinillo	Holmberg	Travaglia	Mercedes
Intercept	0.047	0.009	−0.028	−0.019	−0.000	−0.044	0.016
R²	0.035	0.682	0.771	0.695	0.827	0.779	0.759
d.f.	26	23	19	17	15	23	20
Slopes	0.118	0.480	0.625	0.676	0.647	0.641	0.649
SE	0.122	0.038	0.078	0.108	0.076	0.071	0.082

SE: standard errors of the slope estimates.
d.f.: degrees of freedom.

Table 2. Adjusted fits of the relation between high and low sticky traps, for Toya spp. captures

				Sampling stations			
	Mandredi	Tancacha	Cabrera	Espinillo	Holmberg	Travaglia	Mercedes
Intercept	0.047	0.020	0.116	0.060	0.088	0.037	−0.028
R²	0.201	0.562	0.083	0.641	0.072	0.632	0.862
d.f.	26	23	18	16	15	23	22
slopes	0.811	0.583	0.311	1.950	0.910	2.794	3.177
SE	0.318	0.107	0.243	0.365	0.840	0.454	0.271

SE: standard error of the slope estimates.
d.f.: degrees of freedom.

with maize plots during the maize season. Within the northern area, the land is used mainly for grain production in small plots, with high temporal and spatial heterogeneity as soya beans, peanut and sunflower (not appropriate as a host for the Delphacidae) are cultivated. The abundance of *Toya* spp., may suggest that the former is better adapted for flying longer distances (as it flies higher). If that were true, then it could explain the higher abundance of *D. kuscheli* within the MRDV-RC endemic region, where more abundant and bigger patches of appropriate host (either for the vector feeding, overwintering and/or reproduction) occur.

The differential synchrony of abundance peaks between the two most abundant groups (*D. kuscheli* and *Toya* spp.) deserves special consideration. The field data shows that *D. kuscheli* abundance peaks simultaneously all over the area, whereas *Toya* spp. does not. The cause of the difference is related to the triggering process of the dispersal mechanism. Among the hypotheses explaining this mechanism, density-dependent (DENNO et al., 1991) and density-independent responses (KISIMOTO, 1987) linked to habitat persistence and constrained by migratory ability, have been proposed. A species with high or low dispersal ability, living in persistent habitat homogeneously distributed over space, would have positive selection if the decision to leave the bad patch was based upon the host quality deterioration due to an increase in the abundance of its population (density-dependent response), because the probability of arriving at a 'good' patch is high. Another species living in a temporary habitat, heterogeneously distributed over space, would have positive selection only if the individual leaves the patch as soon it has the ability to do so (i.e. is macropterous), independent of the insect density on that patch.

The fact that *D. kuscheli* disperses simultaneously over large areas, and during a short time period (1–2 weeks), may suggest that its dispersal mechanism is not triggered by a density-dependent mechanism, but that they start flying when the macropterous cohort emerges (synchronized by a temperature–development time). Among the species found during this field study, *D. kuscheli* was shown to be the best disperser. This ability allows the individual disperser reaching distant favourable patches, especially within the MRDV-RC endemic area where pasture plots (the main plant host for the species) are very common. This colonizing ability is greatly reduced outside the endemic area (towards the north-east of the study area), because pasture plots are infrequent and smaller.

In contrast, *Toya* spp. were shown to be worse fliers, with abundance peaks not occurring simultaneously, but instead extending over a longer time period (compared with *D. kuscheli*). This may suggest that they only disperse when the population abundance on a host patch is high enough to decrease the host plant quality, and increasing the chances of a better performance on a different patch, even when their dispersal ability is not as high.

The geographical distribution of the Delphacidae in the study area suggest a highly favourable area within the endemic region, where the most abundant delphacid population are found (especially *D. kuscheli* and *Toya*

spp.). North-east and south-west of this area, favourability decreases, in a more or less concentric shape. Although the field-collected data are not amenable to spatial interpolation (because the study was carried out along a transect, not on a grid), the clustering analysis is consistent with this geographic distribution pattern.

The high dispersal ability suggested by the *D. kuscheli* data, show more important difficulties than previously anticipated on MRDV-RC transmission control. Although as current knowledge indicates, weeds surrounding or within the maize plots may constitute vector sources, the role of weeds may become of relatively minor importance because of the part played by the high dispersal ability of the insect vector and the much more important sources represented by pastures used for cattle breeding, interspersed with maize plots on a larger geographic scale.

Acknowledgements

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